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VARIATION IN FRESH-WATER MUSSELS

GORDON H. BALL

University of Pittsburgh

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INTRODUCTION AND STATEMENT OF THE PROBLEM

Shells of fresh-water mussels are variable with respect to height, length, obesity, the relative proportions of these dimensions, strength of corrugations, intensity of rays, color of epidermis, of nacre, etc. Although various scattered observations in works devoted primarily to other investigations indicate that these variations are not fortuitous, yet it is only recently that any detailed and careful work has been done for the purpose of determining the relationship of such variations to the ecological conditions in which the shells are found.

A brief review of at least some of the observations on the variability of fresh-water mussel shells is necessary. The early systematists, particularly Lea, were inclined to disregard the fact of considerable intra-specific variability and to form a new species for every local variation. Later workers showed the identity of many of these early species, and consequently reduced their number considerably. However, it appears that all the work in this field has not yet been accomplished, and that many forms now described as distinct species are but variations connected with the environmental conditions.

Observations on the variations themselves and their probable dependence on the environment are not very numerous, however. Wetherby (1882) noted that some species vary more than others; and also that shells of mountainous regions are subject to the greatest variety of conditions, since the streams flow through more heterogeneous strata, contain a more variable amount of mineral matter, and, being subject to greater extremes in the rate of flow, transport more different kinds of sediment than is the case with lowland waters. Consequently, he believed that any inherent tendency to vary would be called out in this environment.

Several European investigators have noted that the same species takes different forms in rapid and in quiet waters. Among these may be mentioned Israel (1910), who remarks on the extreme variability of *Unio crassus,* stating that it takes a special form in almost every brook. In slow-flowing brooks with mud bottoms this species is long, with gently curved lower margins, and has a thick crust of mud at the posterior end; in brooks with a strong current and a shale bottom without gravel the shells are shorter, resembling *U. litoralis,* having quite normal posterior markings, with no trace of any slimy encrustation. In the rapid streams the posterior ends of the shells may be stunted by the rather large boulders. He also states that in the same brook the mussels may differ according to the kind of bed and the force of the water; and that, generally speaking, in swift streams or small rapids the mussels are much shortened or truncated, often almost round or bluntly triangular. In streams that are slightly less rapid the shells are somewhat longer and seem to stand between those of swiftly flowing waters and those of quiet pools, even though one or both of the other conditions exist but a few feet away. The type-form is that of the quiet pools; the shape of the others seems to depend upon the movement of the boulders and the more or less firm bed. However, Israel points out that the glochidia of all the different forms, as well as the young shells, are alike, and hence concludes that he is dealing with only a single species.

Isely (1911 and 1913) observed that peculiarities of distribution are very probably to be traced back to the young shells, and that the conditions having most influence on them will be most potent in determining the character of the adults. He also found by experiment that the rate of growth of the shells is very variable for individuals of a single species in the same stream or in different streams, depending on season, food, oxygen supply, and various other conditions. Young mussels grow much more rapidly than older ones, and different species grow at different rates. The growth period is usually from April to September. It would seem, therefore, that environmental conditions, in order to be effective, would have to act on the young shells, and at the favorable period of the year.

Meek and Clark (1912), speaking of *Rotundaria tuberculata,* say that the shells become smaller and thinner downstream, and that the main difference between this species and *R. granifera* is to be found in the degree of inflation. Coker (1914) records a difference in commercial value between shells of the same species found in lakes and in river-lakes, a difference registered mainly in shape and thickness. Wilson and Clark (1914), in their study of the mussels of the Cumberland River and its tributaries, arrived at these conclusions: that of two closely related forms differing mainly in the degree of inflation and both found in the same river system, the flatter and less inflated forms are found in the tributaries and the upper part of the stream; and the more swollen shells are in the lower stretches of the river, where there is a weak current and considerable mud. Secondly, other characters besides inflation are dependent on the rate of stream flow, size of stream, and kind of bottom, so that characters used as specific distinctions at one point become valueless elsewhere. Again, faunas of widely separated tributaries are often quite similar. In other cases a certain species may demand special environmental conditions, and thus its distribution will depend on other factors than mere stream position. Finally, different streams show various degrees of difference between large and small-stream species. These investigators found that the mussels could be separated into four groups: (1) small-stream species, restricted to the upper portions of the river and to its tributaries; (2) large-stream species, restricted to the lower portions of the main river; (3) species universally distributed over the river; and (4) species restricted to a limited region. In particular, they observed the distribution of *Rotundaria tuberculata* and *R. granifera*. Since these forms have been treated at some length in this paper, the observations of Wilson and Clark regarding them will be referred to later. Danglade (1914) made somewhat similar observations in the Illinois River on this species and on *Amblema costata* and *Obliquaria reflexa*. He also observed that the shells tend to become smaller going downstream. While Utterback (1916) states that in the Osage River compressed forms are to be found in the headwaters where the water is shallower and swifter, and that these forms become more swollen and heavier farther downstream where the water is deeper and more sluggish. Adams, in his investigations of the fresh-water gastropod *Io* (1915), also observed changes in various shell-dimensions in relation to position on the stream. He found, in addition, that the size of the stream apparently influenced the size of the shell; in this case small shells were found in small streams and large shells in large streams.

The first work devoted solely to the study of the variations of the shells of fresh-water mussels appears to have been that of Grier (1920*a*). He compared certain shells of Lake Erie with corresponding species of the Upper Ohio, and found several apparent correlations between various morphological features and the environment. The Lake Erie shells tended to have broader growth-lines, brighter colors, and a more polished epidermis, and to be smaller and thinner. Specifically, he found that practically all the shells he examined were more inflated in Lake Erie, had a greater posterior development, a better developed posterior hinge-length, and less thick valves than the forms in the Ohio. The height of the shell appeared to vary independently of the environment. The size of the members of the groups, as a whole, apparently varied directly with the size of the stream. This does not agree with the results of Danglade (1914) and of Meek and Clark (1912), who found the larger shells in the smaller streams. Further studies were made by Grier on correlation of morphology and sex (1920*b*), of nacreous color and station (1920*c*), and of epidermal color and station (1920*d*). He found with regard to sex certain apparent correlations with morphological features; many of these results, however, can not be considered significant owing to the lack of a sufficient number of cases. Taking the five species in which more than fifteen shells were considered, he found that the female shells, on the whole, were more inflated and higher with a greater length of the anterior hinge-line. In *Fusconaia flava, Amblema plicata,* and *Lampsilis luteola,* the female also had a greater posterior development and a thicker shell, while the opposite held true for *Eurynia recta* and *Lampsilis ovata.* Grier's conclusions in his study of nacreous color were that the nacre tended to vary in color considerably more than is ordinarily recorded; that it tended to become lighter or more bluish going downstream, with the Lake Erie shells having a greater proportion of blues than those of the Upper Ohio or Maumee; that there was probably a peculiar kind of nacre for each drainage or for certain localities in a single drainage; and that nacreous color appeared to be correlated with sex, but not with age. Regarding epidermal colors, the same conclusions were found concerning large amount of variability, effect of the drainage basin and locality on epidermal color, and correlation with sex. There was no connection between age and color except that the older shells tended to become darker. The epidermis tended to darken going downstream and was darker in the Upper Ohio and Maumee than in Lake Erie. Rays were best developed in small streams, and disappeared with age.

As early as 1909 Ortmann had made similar observations regarding obesity and stream position. In his paper on the fresh-water mussels of the Tennessee drainage (1918), he noted that in certain shells a flat and compressed form was found in the headwaters, a swollen form in the large rivers, and an intermediate form in rivers of medium size. He used this difference in obesity as a distinguishing characteristic, putting the shells in certain varietal groups according as they measured more or less than a certain arbitrary figure. He carried this out for several species groups, finding in many cases that the form originally described and bearing the species name was really intermediate in so far as obesity was concerned. Later he made a special study (1920) of this apparent correlation of obesity and position on the stream in several species groups. Those which he found to be connected by intergrades he made one species with several varieties. In addition to confirming his former conclusions regarding decrease in obesity in the headwaters, he found that young shells on the average were more swollen than older ones; that less obese shells were frequently longer; and that a tuberculated form frequently lost its tubercles in the headwaters. On the other hand, he found many species that showed no trace of this greater obesity in larger streams, being approximately equally swollen along the whole river system. In a recent letter to Dr. Ortmann, Danglade confirms many of these conclusions. In particular, he finds that *Lampsilis anadontoides* and *L. fallaciosa* are not associated together to any noticeable extent, the former preferring the lower stretches of the large rivers and a shore bar of gravel or sand, while the latter seeks quiet waters and a soft or mud bottom near shore. He finds, differently from Grier, that those shells with clearer markings and more rays come from muddy streams where they are more or less hidden from the light. A great many other characters besides rapidity of flow and character of bottom affect the features of the shells, but, in general, swifter waters and harder bottoms mean more compressed shells, lighter epidermis, and lighter nacre. Danglade found this to hold true not only for the above-mentioned *anodontoides* and *fallaciosa,* but also for *Obliquaria reflexa, Obovaria olivaria, Megalonaias heros, Rotundaria tuberculata, Lampsilis ovata ventricosa,* and *Actinonaias carinata* (*ligamentina*).

In nearly all the above statements, the conclusions have been based on general observations rather than on accurate mathematical measurements. The only exceptions are the papers of Grier and of Ortmann (1920). Even here nothing beyond maxima, minima, and means of the shell dimensions have been considered. In one case the shells are grouped into those from Lake Erie and those from the Upper Ohio, and in the other computations are based on the shells taken from one locality regardless of the number of specimens. Nowhere has any treatment been made of the subject in which the environmental factors have been measured so that accurate mathematical proof of these above statements could be obtained, and actual correlation of shell variations and the environment be shown to exist.

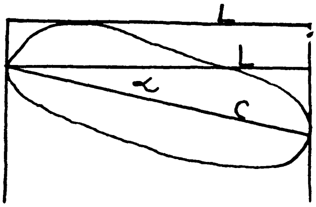
The problem of this paper, then, really falls into two parts. First, to treat certain variations of the shells of fresh-water mussels in such a way that the dependence or lack of dependence of these variations on certain factors of their environment can be proved statistically. And, secondly, to show that several forms originally described as separate species are, in reality, only geographical or ecological races, differing from one another mainly in the degree of obesity, and abundantly connected by intergrades.

Method

The material used was from the collection of the Carnegie Museum, Pittsburgh, Pa., Dr. W. J. Holland, director. The work was done under the guidance of Dr. A. E. Ortmann, who suggested the problem and the species to be used, and assisted in every possible way during the progress of the work. I wish to express my great appreciation to him for his aid in the preparation of this report. To Professor H. D. Fish, of the Department of Zoology of the University of Pittsburgh, I desire to make acknowledgment for his suggestions regarding the statistical treatment of the data. I wish also to express my gratitude for the aid that has come to me from other sources.

Approximately 1,150 shells were considered; these belong to the following species-groups:

1. *Amblema peruviana.*
2. *Amblema perplicata.*
3. *Rotundaria tuberculata.*
4. *Ptychobrànchus occidentale.*
5. *Ptychobranchus greenii.*
6. *Lampsilis orbiculata.*
7. *Truncilla torulosa.*
8. *Truncilla rangiana.*



Only those shells were considered the locality of which was known, a locality meaning—in practically every case—a definite point on a certain stream. The length and diameter of every shell were measured in tenths of a millimeter by means of a vernier caliper. The length was taken parallel to the hinge-line; the diameter was the greatest distance at right angles to this measured from left to right. The obesity was then found by dividing the diameter by the length and reducing to a percentage basis. In addition, the height, taken at right angles to the length, and measured dorso-ventrally, was taken for *Ptychobranchus occidentale* and *Lampsilis orbiculata.* The greatest length of the shell was also taken for the former species; and the distance from the dorsal margin to the point of greatest inflation for the latter. The reasons for taking these measurements will be brought out under the discussion of results. For all the *Truncillas,* the prominence of the tubercles was also estimated by means of an arbitrary grading scale. Wherever possible, the age and sex were noted for each shell; and, in certain species, the color of the nacre, of the epidermis, the relative smoothness, prominence of ridges, etc. The shells were then arranged and tabulated by localities, beginning downstream and going up each tributary as one arrived at it. In order to reduce the environmental factors to a statistical basis, it was decided to attempt to correlate these variations with stream-flow measurements. These measurements have been taken for several years by the United States Geological Survey and by various state commissions. Wherever possible, yearly averages were computed for all readings taken from 1899 to 1920 at all localities from the stream-flow of which might be obtained that of points where shells were available. The main source of information was the annual Water Supply Papers of the U. S. Geological Survey. These give measurements in cubic feet per second (second-feet), and are based on the size of the streambed and on the rate of flow. Maps were then made up, on which were indicated the points from which shells had been obtained, and the stations at which stream-flow measurements were available. By this means it was possible, in practically every case, to find a fairly accurate stream-flow measurement for a locality possessing shells. For several cases the stream-flow in five hundred second-feet was plotted on quadrille-ruled paper against the obesity in five tenths of a percent. These tables were then condensed, owing to the manner in which the shells were grouped, by setting up the following divisions based on size of stream-flow.

0–749 second-feet.
750–1,749 second-feet.
1,750–3,249 second-feet.
3,250–8,249 second-feet.
8,250–25,249 second-feet.
25,250–40,249 second-feet.
40,250 and above second-feet.

Against this was plotted the obesity in groups of two percent, or the arbitrary factor for tubercle development, etc. In this way each measurement was recorded separately (figures 1 and 4 illustrate this method of setting

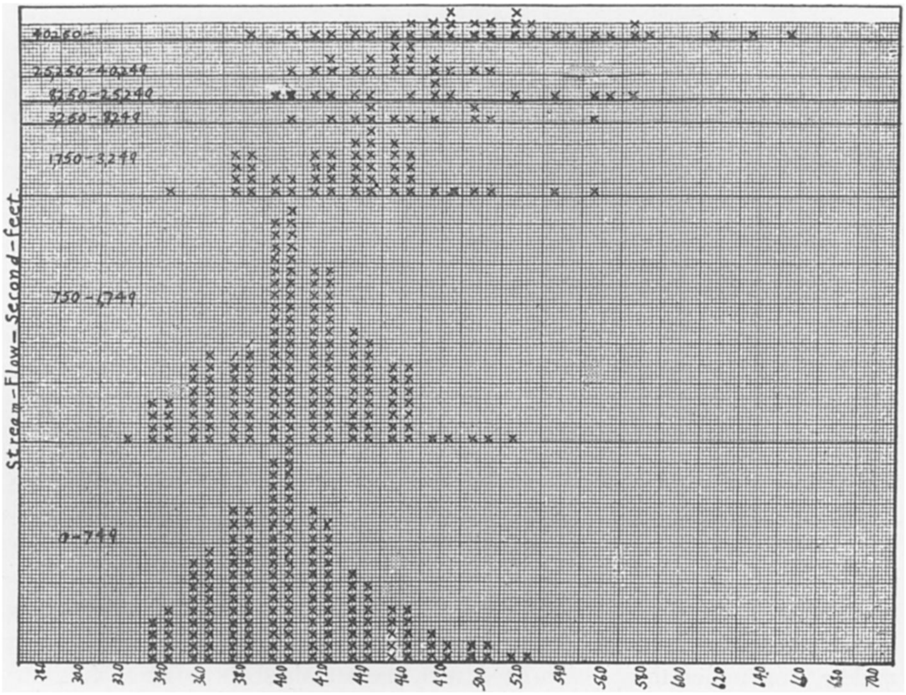


FIG. 1. Distribution of obesity in the *Amblema peruviana* group. Each shell is represented by an 'x'. The tendency for the shells to become more obese in the larger streams is clearly shown.

down the results). In those species where the sex of a large number of shells was known, the shells were plotted in the usual manner and then plotted separately by sexes to discover any correlation based on sex differences (illustrated in figure 5). For the majority of these groups, the mean and the average deviation, as well as the probable error of both, were computed. The summary of these results is found in Tables I to IV. Curves were then drawn, based on these computations, for the mean and for the mean plus and minus the standard deviation. Smooth curves were then drawn on the same sheets to show the general trend of the variations regardless of fluctuations due to insufficient data (figure 2 is an example).

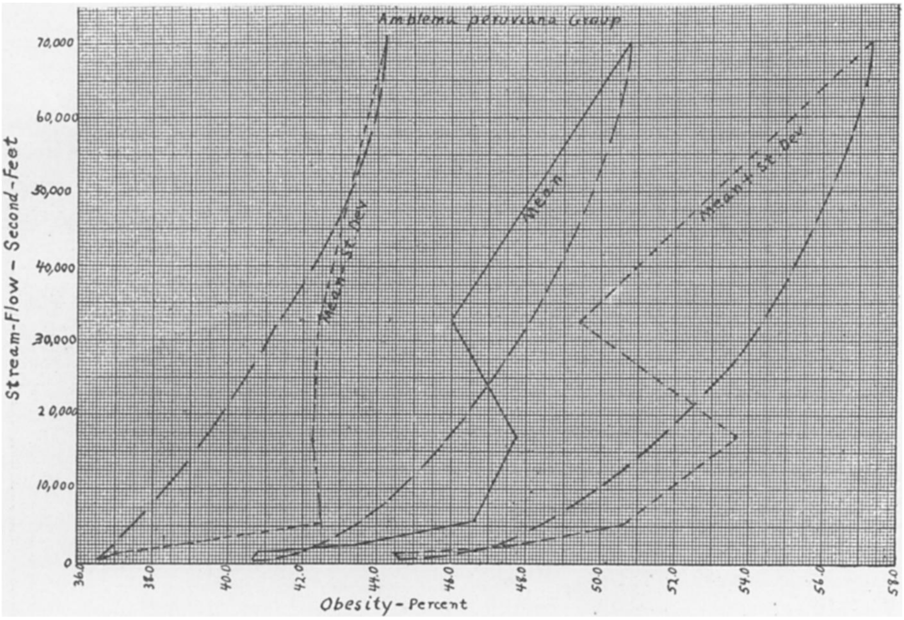


FIG. 2. Mean obesities (middle curve), mean plus standard deviation (right), and mean minus standard deviation (left), for all shells of the *Amblema peruviana* group, plotted for different sized streams. The data are the same as for figure 1, but are illustrated differently. The smoothed curves show the general tendency of the readings.

In order to determine whether or not the longer and hence the older shells were more swollen than the shorter or younger ones, approximately one hundred shells were taken in each species-group from a few localities, allowance being made for differences due to variations in amount of stream-flow. These shells were arranged according to length; and the obesity of the lower, middle, and upper thirds calculated with the standard deviations, as shown in Table II. Stepped curves for these means were then drawn (illustrated in figure 3).

The classification used was that of Ortmann (1912). Wherever closely

TABLE I. *Size of shells in relation to size of streams in which the shells were found. Shell size expressed in obesity percent, stream size in second-feet of stream flow* For each species the upper row of numbers represents mean obesity minus standard deviation; the middle row is mean obesity; the lowest row is mean obesity plus standard deviation.

Species group	Stream flow in second-feet						
	0–749	750–1749	1750–3249	3250–8249	8250–25249	25250–40249	40250–
	Obesity Percent						
Amblema peruviana	36.627	37.182	39.112	42.477	42.004	42.446	44.198
	40.613	40.836	43.362	46.667	47.867	46.0	50.727
	44.599	44.490	47.612	50.857	53.730	49.554	57.256
Amblema perplicata	45.042	42.672	47.877	47.610	48.322		
	48.133	48.435	51.889	50.0	53.149	....	....
	51.224	54.198	55.901	52.390	57.976		
Rotundaria tuberculata	42.403	41.665	43.970	44.163	42.182	48.352	49.321
	49.714	46.714	49.440	49.0	47.714	51.333	55.2
	55.945	51.763	54.910	53.837	53.247	54.314	61.079
Ptychobranchus occidentale	25.557		25.860	34.0			
	31.294		32.782	35.0	....	....	....
	37.031		39.704	36.0			
Ptychobranchus occidentale ∝	1.786		7.173	8.8			
	5.306		11.766	9.9	....	....	....
	8.826		16.359	11.0			
Ptychobranchus greenii	35.640	33.222	....	35.901	37.584		
	37.6	36.182	....	38.5	40.7	....	....
	39.560	39.142	....	41.099	43.816		
Lampsilis orbiculata			45.084	....	39.564	49.816	45.619
			51.0	....	47.334	54.640	50.667
			56.916	....	55.104	59.464	55.715
Lampsilis orbiculata ♂			46.734	....	40.764	50.0	44.226
			50.0	....	43.0	51.0	48.462
			53.266	....	45.236	52.0	52.698
Lampsilis orbiculata ♀			43.706	....	40.305	52.310	50.734
			51.5	....	50.0	56.286	54.0
			59.294	....	59.695	61.342	57.266
Truncilla torulosa	36.927	39.353	42.064	44.315	54.369	50.0	47.261
	39.556	41.0	45.8	47.440	54.667	50.0	50.133
	42.185	42.647	49.536	50.565	54.965	50.0	53.005
Truncilla torulosa ♂	36.716	39.858	44.980	46.612	54.369	50.0	48.735
	39.5	41.250	47.667	48.667	54.667	50.0	50.0
	42.284	42.642	50.354	50.722	54.965	50.0	51.265
Truncilla torulosa ♀	40.0	40.0	39.683	39.508	....	....	49.461
	40.0	41.0	43.0	46.308	....	....	52.4
	40.0	42.0	46.317	53.113	....	....	55.339
Truncilla torulosa. Tubercles	1.196	.834	1.060	1.409	4.0	6.0	4.914
	1.667	1.286	1.7	2.120	4.0	6.0	5.533
	2.138	1.738	2.340	2.831	4.0	6.0	6.152
Truncilla rangiana	45.839	44.254	44.174	....	47.533		
	48.667	47.838	46.476	....	49.889	....	....
	51.495	51.422	48.778	....	52.245		
Truncilla rangiana ♂	48.586	45.181	45.940	....	47.872		
	50.0	47.905	47.739	....	50.154	....	....
	51.414	50.629	49.538	....	52.436		
Truncilla rangiana ♀	43.929	43.033	44.881	....	46.8	....	....
	47.5	47.333	46.861	....	49.2	....	....
	51.071	51.633	48.841	....	51.6	....	....
Truncilla rangiana. Tubercles	1.196	1.181	1.256	....	1.574		
	1.667	1.703	1.881	....	1.889	....	....
	2.138	2.225	2.506	....	2.204		

related species were found to differ mainly in degree of obesity, due to differences in the size of streams, and intergrades were found in streams of intermediate size, these forms were considered as one species. However, when there was a sharp break in the degree of obesity, and this break was not connected with a difference in stream-flow; or when, for the same size streams, the obesity in one drainage was obviously different from that in another, specific names were retained. In order to avoid disputes regarding synonymy, shell measurements by various investigators were recorded and the obesity determined. Only those measurements were used which clearly had been obtained in a way similar to that used in this report. In those cases where the shells had been measured differently, as in Lea, and wherever else possible, the illustrations themselves were measured and the required percentages calculated. Lines of separation, based on degree of obesity, were more or less arbitrarily drawn, but no other procedure was possible in a series of intergrading forms.

TABLE II. *Relation of obesity percent to shell-length*

For each species the upper row of numbers represents mean obesity minus standard deviation; the middle row is mean obesity; the lowest row is mean obesity plus standard deviation.

Species group	Shell length		
	Shortest third	Middle third	Longest third
	Obesity Percent		
Amblema peruviana	*38.756*	*45.230*	*37.058*
	41.650	41.949	40.3
	44.544	*38.668*	*43.542*
Amblema perplicata	*45.656*	*46.817*	*45.081*
	53.438	52.848	49.875
	61.220	*58.879*	*54.669*
Rotundaria tuberculata	*49.018*	*44.436*	*40.307*
	56.4	50.412	44.571
	63.782	*56.388*	*48.835*
Ptychobranchus occidentale	*25.527*	*27.864*	*25.581*
	30.857	35.143	30.857
	36.187	*42.422*	*36.133*
Ptychobranchus greenii	*37.548*	*36.462*	*35.895*
	41.308	39.077	38.077
	45.068	*41.692*	*40.259*
Lampsilis orbiculata	*43.2*	*48.255*	*47.671*
	50.4	54.0	52.480
	57.6	*59.745*	*57.289*
Truncilla torulosa	*40.216*	*44.5*	*41.102*
	45.571	48.852	46.143
	50.926	*53.204*	*51.184*
Truncilla rangiana	*44.761*	*41.691*	*44.208*
	47.714	48.667	47.829
	50.667	*55.643*	*51.450*

TABLE III. *Summary of shell measurements in relation to stream-flow, showing probable error, standard deviation, and probable error of standard deviation*

M = Mean obesity, and probable error of mean. *s* = Standard deviation and probable error of standard deviation.

Species group	Stream-flow in second-feet						
	0–749	750–1749	1750–3249	3250–8249	8250–25249	25250–40249	40250——
	Obesity Percent						
Amblema peruviana..........	*M*40.613± .219	40.836± .204	43.362± .418	46.667± .815	47.867±1.021	46.0 ± .550	50.727± .767
	s 3.986± .165	3.654± .144	4.250± .396	4.190± .577	5.863± .722	3.554± .411	6.529± .542
Amblema perplicata..........	*M*48.133± .602	48.435± .573	51.889± .451	50.0 ± .609	53.149± .870		
	s 3.091± .426	5.763± .405	4.012± .319	2.390± .431	4.827± .615		
Rotundaria tuberculata..........	*M*49.714± .996	46.714± .526	49.440± .738	49.0 ± .730	47.714±1.410	51.333± .821	55.2 ± .627
	s 6.771± .705	5.049± .372	5.470± .522	4.837± .516	5.533± .997	2.981± .581	5.879± .443
Ptychobranchus occidentale......	*M*31.294± .939		32.782± .973	35.0 ± .675			
	s 5.737± .664		6.922± .688	1.0 ± .338			
Ptychobranchus occidentale ∝ ...	*M* 5.306± .576		11.766± .646	9.9 ± .525			
	s 3.520± .407		4.593± .457	1.1 ± .371			
Ptychobranchus greenii..........	*M*37.6 ± .591	36.182± .602	....	38.5 ± .438	40.7 ± .323		
	s 1.960± .418	2.960± .424	....	2.599± .310	3.116± .235		
Lampsilis orbiculata..........	....	....	*M*51.0 ±1.411	....	47.334±1.747	54.640± .651	50.667± .655
	....	....	*s* 5.916± .997	....	7.770±1.235	4.824± .460	5.048± .463
Lampsilis orbiculata ♂........	....	....	*M*50.0 ±1.272	....	43.0 ± .754	51.0 ± .675	48.462± .792
	....	....	*s* 3.266± .900	....	2.236± .533	1.0 ± .338	4.236± .560
Lampsilis orbiculata ♀........	....	....	*M*51.5 ±2.629	....	50.0 ±3.270	56.286± .814	54.0 ±1.886
	....	....	*s* 7.794±1.859	....	9.695±2.312	4.516± .576	3.266± .734
Truncilla torulosa..........	*M*39.556± .591	41.0 ± .297	45.8 ± .797	47.440± .422	54.667± .116	50.0 ±0	50.133± .242
	s 2.629± .417	1.647± .210	3.736± .563	3.125± .298	.298± .082	0	2.872± .171
Truncilla torulosa ♂..........	*M*39.5 ± .664	41.25 ± .332	47.667± .739	48.667± .401	54.667± .116	50.0 ±0	50.0 ± .566
	s 2.784± .470	1.392± .235	2.687± .523	2.055± .283	.298± .082	0	1.265± .270
Truncilla torulosa ♀..........	*M*40.0±0	41.0 ± .675	43.0 ±1.119	46.308±1.273	....	....	52.4 ± .886
	s 0	1.0 ± .338	3.317± .791	6.805± .900	....	....	2.939± .627
Truncilla torulosa. Tubercles...	*M* 1.667± .106	1.286± .081	1.7 ± .137	2.12 ± .096	4.0 ±0	6.0 ±0	5.533± .108
	s .471± .075	.452± .058	.640± .097	.711± .068	0	0	.619± .076
Truncilla rangiana..........	*M*48.667± .636	47.838± .421	46.476± .240	....	49.889± .374		
	s 2.828± .449	3.854± .297	2.302± .169	....	2.356± .265		
Truncilla rangiana ♂.........	*M*50.0 ± .477	47.905± .4	47.739± .252	....	50.154± .427		
	s 1.414± .337	2.724± .283	1.799± .179	....	2.282± .302		
Truncilla rangiana ♀.........	*M*47.5 ±1.205	47.333± .749	46.861± .306	....	49.2 ± .724		
	s 3.571± .851	4.3 ± .529	1.98 ± .217	....	2.4 ± .512		
Truncilla rangiana. Tubercles..	*M* 1.667± .106	1.703± .059	1.881± .065	....	1.889± .050		
	s .471± .075	.522± .042	.625± .046	....	.315± .035		

RESULTS

Tables I and II summarize the mean obesities, and the means plus and minus the standard deviations, in relation to stream-flow and shell length.

Tables III and IV summarize the means and standard deviations, with the probable errors of each.

TABLE IV. *Relation of obesity percent to shell-length, showing probable error, standard deviation, and probable error of standard deviation*

M = Mean obesity and probable error of mean.
s = Standard deviation and probable error of standard deviation.

Species group		Shell length		
		Shortest third	Middle third	Longest third
		Obesity Percent		
Amblema peruviana	*M*	41.650±.309	41.949±.354	40.3 ±.346
	s	2.894±.218	3.281±.251	3.242±.218
Amblema perplicata	*M*	53.438±.928	52.848±.708	49.875±.572
	s	7.782±.656	6.031±.501	4.794±.404
Rotundaria tuberculata	*M*	56.4 ±.842	50.412±.691	44.571±.486
	s	7.382±.595	5.976±.489	4.264±.344
Ptychobranchus occidentale	*M*	30.857±.961	35.143±1.312	30.857±.951
	s	5.330±.679	7.279±.928	5.276±.673
Ptychobranchus greenii	*M*	41.308±.444	39.077±.346	38.077±.289
	s	3.760±.314	2.615±.245	2.182±.204
Lampsilis orbiculata	*M*	50.4 ±.971	54.0 ±.791	52.480±.649
	s	7.2 ±.687	5.745±.559	4.809±.459
Truncilla torulosa	*M*	45.571±.683	48.852±.565	46.143±.643
	s	5.355±.483	4.352±.399	5.041±.454
Truncilla rangiana	*M*	47.714±.337	48.667±.784	47.829±.413
	s	2.953±.238	6.976±.554	3.621±.292

1. Group of *Amblema peruviana* (Lamarck). (437 shells.)

(*a*) **Amblema peruviana costata** (Rafinesque). Obesity 47 percent or less.

Unio costatus Conrad, 1836. Obesity 43.0.
Quadrula undulata Baker, 1898. Obesity 38.0; 38.4; 39.7; 40.0.
Quadrula undulata Simpson, 1914. Obesity 30.9; 36.4; 42.8.
Quadrula costata Vanatta, 1915. Obesity 36.4.

Here also belong two of the forms described by Simpson as *Quadrula plicata,* with obesity of 45.4 and 38.4.

(*b*) **Amblema peruviana** (Lamarck). Obesity over 47 percent.

Quadrula plicata Baker, 1898. Obesity 63.4; 65.0.
Quadrula plicata Simpson, 1914. Obesity 57.8.

Two other forms called *plicata* by Simpson belong under *costata.* However, the average of Simpson's three forms amounts to 47.2.

Unfortunately, *A. peruviana* is the variety, and *costata* the original form, but priority in nomenclature compels use of this terminology. *Amblema peruviana* is the more swollen type of the larger rivers with smooth bottoms; there is a complete series of intergrades with the less obese *costata* of the smaller and more rapid streams with gravel or sandy bottoms. *Peruviana* is to be found in the Ohio and Mississippi drainages; it is mainly found in streams of considerable size and possesses high beaks and few undulations.

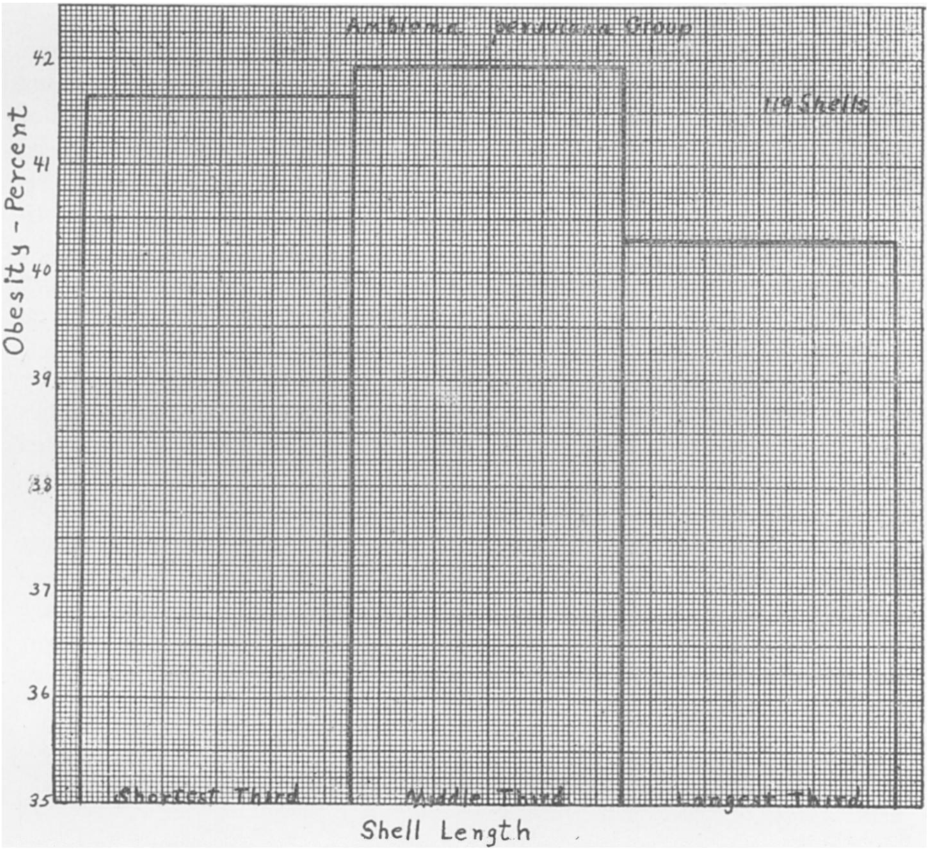


FIG. 3. Obesities of the longest, the middle, and the shortest thirds of 119 shells of the *Amblema peruviana* group. There is a tendency for the longest, hence the oldest, shells to be less obese.

Rafinesque's type form of *costata,* measured by Vanatta, is described as coming from a small creek in Kentucky. This variety is less swollen, has less prominent beaks, and is usually more undulated than *peruviana;* there are practically no other distinctions between the two forms. Conrad's point that *A. costata* has a more yellowish epidermis does not seem to hold when large numbers of shells are considered. Figure 1 and Tables I to IV show the dependence of the degree of obesity in this form upon the size of the stream-flow. It should be noted in this connection that four of the six *A. peruviana* found in streams of 1,750–3,250 second-feet come from the Ohio Canal at Columbus, Ohio. Here, although the stream-flow measured in second-feet is small, large-river conditions are present; for example, smooth, slowly flowing water and an even bed. It is just such an exception as this which goes far to prove the law that in this group of *Amblemas* smooth beds and slow, even-flowing streams result in more swollen forms than rugged beds and rapid waters. Furthermore, seven of the eleven *peruviana* from the smallest size streams come not from headwaters, but from small streams such as the Flint and Paint Rock Rivers and their tributaries not far from Florence, Alabama. These empty into the lower Tennessee at a point where the latter attains great size and possesses shells that are quite swollen. Although Isely has shown (1913) that mussels of this group are not given to excessive migration under favorable conditions, yet migration seems to be the most plausible explanation for the occurrence of these more swollen forms in streams of such small size. This distribution may be due to transportation of the glochidia by fish.

The fact that higher beaks and fewer undulations go with greater obesity are probably nothing more than growth phenomena. As the shell becomes more swollen the beaks will naturally become more prominent and be carried farther forwards, and it is quite likely that this would result also in a smoothing out of the wrinkles or undulations.

The material was deemed insufficient to attempt any correlation of sex and obesity since the sex of but a few of the shells was known. The changes occurring in the color of the nacre and of the epidermis in this species have been investigated by Grier (1920*c* and *d*). A curve for 119 shells shows that, to some degree at least, younger shells of this group are more swollen than older ones (figure 3).

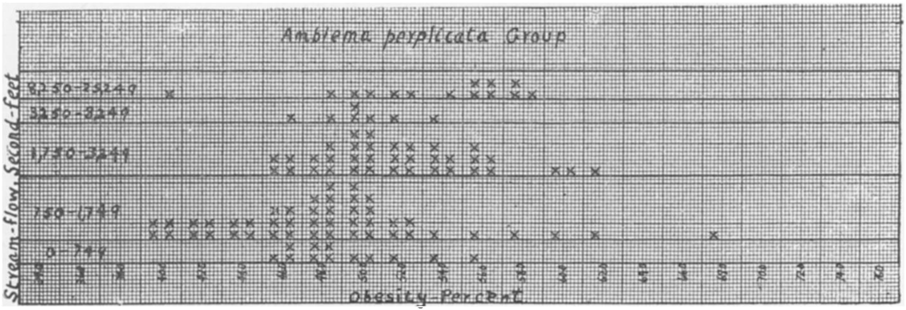


FIG. 4. Distribution of obesity in the *Amblema perplicata* group. A comparison of this figure with figure 1 shows the greater obesity of the *perplicata* as a whole, for the same size streams, as compared with the *peruviana* group.

2. Group of *Amblema perplicata* (Conrad). (153 shells.)

(*a*) **Amblema perplicata elliottii** (Lea). Obesity 53 percent or less.
Unio elliottii Lea, 1858. Obesity 51.9.
Quadrula elliottii Simpson, 1914. Obesity 51.5.

One of the forms of *Quadrula perplicata* of Simpson belongs here. Obesity 41.4.

(*b*) **Amblema perplicata** (Conrad). Obesity more than 53 percent.
Unio perplicatus Conrad, 1850. Obesity —. (Original description, 1841.)
Unio atro-costatus Lea, 1848. Obesity 56.0.
Unio brazosensis Lea, 1869. Obesity 53.6.
Unio lincecumii Lea, 1869. Obesity 58.8.
Unio pauciplicatus Lea, 1874. Obesity 53.5.
Quadrula perplicata Simpson, 1914. Obesity 63.3.

The other form given by Simpson is *elliottii.*

The main difference between these two forms is the smaller degree of obesity for *elliottii.* Intergrading forms are quite common; the more swollen forms are found, as a general rule, in the larger streams; the more compressed *elliottii* in the headwaters. This group is confined mainly to streams flowing into the Gulf of Mexico, particularly in Alabama and Texas. This includes also the southern portion of the Mississippi and its tributaries, as well as a few more northern but western Mississippi tributaries, such as the Missouri River. Lea gives as his localities streams in Georgia, Alabama, Louisiana, and Texas.

Although the shells of the smaller streams are, as a whole, less swollen, yet there is a certain important exception which goes far to show the kind of conditions necessary to produce obesity-conditions, which it should be remembered are found in large streams. Twenty-one shells from the "Old River" of the Ouachita at Arkadelphia, Clark County, Arkansas, are not shown in figure 4 or in the curves. The "Old River" of the Ouachita is an ox-bow of the main stream and is entirely cut off from it at low water. Here lacustrine or large-stream conditions obtain, and we should expect from our knowledge of previous cases that more swollen forms would be found here. This is exactly the case; the shells from this part of the stream have a high degree of obesity, the mean of the group being 59.646, approximately 10 percent greater than the mean of the other shells in streams of similar size. For this reason it has been thought advisable to leave this set of shells out of the calculations. However, the occurrence of such a phenomenon only makes the case stronger. Furthermore, these twenty-one shells are as swollen as any large-stream *A. peruviana.*

In obesity, independent of size of stream, the group of *A. perplicata* is intermediate between *A. peruviana costata* and *A. peruviana.* The form called *elliottii* is closer to *costata; A. perplicata* is nearer *peruviana*. The reason why the *perplicata* group is not united with the *peruviana* group is that, when compared for streams of equal size, the former group is no longer intermediate. *A. perplicata elliottii* is more swollen than *A. peruviana costata,* but it is not found in larger streams; *A. perplicata* is nearly as swollen as *A. peruviana,* but it is found in very much smaller rivers. A comparison of figure 1 and figure 4, and of the means for the two species groups will show this fundamental difference. There is appended a list of the means of the two groups for the same size streams, which makes clear the greater obesity of *A. perplicata* as compared with the other group.

Stream-flow	*A. peruviana*	*A. perplicata*
0–749	40.613	48.133
750–1,749	40.836	48.435
1,750–3,249	43.362	51.889
3,250–8,249	46.667	50.0
8,250–25,249	47.867	53.149
25,250–40,249	46.0	— —
40,250——	50.727	——

What is the reason for this discrepancy? Why should shells of the Coosa River, for example, grow more swollen in tributaries of the same size than the shells of the Tennessee drainage, only a comparatively few miles away? Or why should shells of approximately the same geographical latitude be larger in streams flowing into the southern portions of the Mississippi than in streams tributary to the northern Mississippi? The distribution and the slight but distinct difference between these two species groups suggest a geographical separation in the past into two stocks of an originally homogeneous species. What basis is there for this conclusion when we consider the history of these streams?

The anomalous position of the shells of the Alabama drainage was pointed out by Wetherby (1882) and by Simpson (1900*a*), and the suggestion was made that the Tennessee and the Coosa were once connected. However, it seems probable that the separation took place fairly long ago, and that since Cretaceous times the Tennessee has flowed west at Chattanooga and not south. Ortmann (1912*b*) has shown that the streams west of the Alleghenies in the northeastern part of the country flowed north and northwest in Tertiary times. At this period there was no lower Mississippi River, the present Mississippi, Missouri, and Ohio Rivers being comparatively recent, due to the glacial invasion. He points out that the Allegheny Plateau is continued toward the southwest as the Cumberland Plateau; the latter, although interrupted by the present Mississippi Valley, appears to be connected with the old Ozarks, which extend to the Rockies. This was probably once a continuous elevation and formed the southern boundary of the interior basin.

This basin, being also bounded on the east by the Allegheny Mountains and on the west by the Rockies, had an outlet only to the north. Ortmann believes that the present Tennessee and Cumberland Rivers were the headwaters of the northward-flowing streams of the Tertiary. The Glacial Period resulted in the changing of this drainage; the overflow of the resultant lakes being toward the south and southwest, the present system was formed nearly as constituted today. A study of the crayfishes (*Cambarus*) and of the fresh-water mussels was made by Ortmann, who found the following groups of fauna. The interior fauna is evidently the oldest; migrants from this region established themselves on the Atlantic Coast. One group migrated across the Alleghenian Divide; another group evidently went along the Erigan River, one of the northern outlets, but did not reach farther south than the Carolinas; while still another group probably arose on the southern Atlantic slope, or on the Gulf Plain, and migrated north along the Atlantic Coast or was confined to the southern portion of the Mississippi Valley. And, finally, there was the St. Lawrence fauna.

This brief account of the geologic history of the interior basin is offered in partial explanation of the distribution of *A. perplicata* and of *A. peruviana*. These two forms are different, very probably because they were inhabitants of quite distinct drainage systems as far back as the Tertiary. A divide separated the interior-basin streams from those flowing into the Gulf; and the Ozarks were a barrier between the Red River and the streams farther north. The occasional occurrence of *perplicata* west of the Mississippi, in the Missouri basin, may be explained by the fact that the Mississippi itself, as well as the Missouri, are effective barriers against the migration of mussels.

It has been suggested that the resemblance between the fauna of the Tennessee and of the Coosa is due to an original connection between the two streams. However, this slight resemblance does not necessarily prove a common drainage basin. Such distributional phenomena might be due to quite recent stream-capture, the tributaries of the Coosa encroaching upon those of the Tennessee, or they might be the result of transportation by various agencies. It is enough to show that these drainage basins were at one time distinct to offer a possible explanation of the differences in their fauna.

The measurements of 97 shells show that for this group also the younger shells are more swollen than the older ones.

3. Group of *Rotundaria tuberculata* (Rafinesque). (169 shells.)
    (*a*) **Rotundaria tuberculata** (Rafinesque). Obesity 57 percent or less.
        Unio tuberculatus Conrad, 1836. Obesity 53.5.
        Quadrula verrucosa Baker, 1898. Obesity 42.2♀; 41.8♂.
        Quadrula tuberculata Simpson, 1914. Obesity 36.8; 44.0; 46.7.
        Quadrula tuberculata Vanatta, 1915. Obesity 49.2.
    (*b*) **Rotundaria tuberculata granifera** (Lea). Obesity more than 57 percent.

Unio granifera Lea, 1838. Obesity 72.1.
Quadrula granifera Simpson, 1914. Obesity 58.4; 71.7.

The differences between these two forms are in degree of obesity and number and prominence of tubercles. *Granifera* is more swollen and more tuberculated than *tuberculata,* and is frequently smaller. The reduction in size appears to bear out the statement of Ortmann (1920) that more swollen shells make up for their greater obesity by being shorter than the flatter shells. The distinction based upon strength of tubercles is not clear-cut and does not seem to be closely correlated with obesity. Simpson and Lea disagree about the relative prominence of the tubercles; the former says that those of *granifera* are stronger, the latter that they are smaller. Lea's specimen of *granifera* came from the Ohio River near Cincinnati; and Rafinesque's *tuberculata* from the Ohio River, no definite locality being given. Conrad states that this species is not found in Alabama south of the Tennessee River and its tributaries—another instance of the peculiarity of the fauna of the Coosa, Cahaba, etc.

Wilson and Clark (1914) have already suggested that *tuberculata* and *granifera* are connected by intergrades, the obesity depending on the size of the stream. The present investigation shows this to be the case, the larger *granifera* being practically confined to the larger streams. All cases of its occurrence in streams of less than 1,750 second-feet are in those rivers that are tributary to the Tennessee near Florence, Alabama, and can be explained as the result of migration from the broader and deeper Tennessee. A similar case was pointed out in discussing the *Amblema peruviana* group.

To a very decided degree young shells of this group are more swollen than older ones.

4. Group of *Ptychobranchus occidentale* (Conrad). (42 shells.)

Lack of a sufficient number of shells makes it impossible to state definitely the facts in this case. However, based on the material at hand, the following purely tentative suggestions are made.

If obesity is used as a basis of classification, the following groups can be set up:

(*a*) **Ptychobranchus occidentale clintonense** (Simpson). Obesity 32 percent or less.
Ptychobranchus clintonensis Simpson, 1900. Obesity 30.1.
Ptychobranchus clintonense Simpson, 1914. Obesity 31.1.

(*b*) **Ptychobranchus occidentale** (Conrad). Obesity over 32 percent.
Unio occidentalis Conrad, 1836. Obesity 32.7.
Lampsilis occidentalis Simpson, 1914. Obesity 37.5 ♀; 39.9 ♀.

However, these two forms do not differ only in obesity; the more swollen form has the beak pushed far forward, producing a "hump." The flatter forms are not humped. The amount of displacement of the beak can be measured in degrees and recorded. This group might then be divided into those forms having a hump of 10 degrees or less, and those with a hump of over 10 degrees. However, a measurement of Conrad's figure for *Unio occidentalis* shows no displacement or a value of 0 degrees. On the basis of this, we should be forced to make *occidentale* the flat form, of which *clintonense* is just a synonymous term. Although the amount of displacement of Simpson's *clintonense* is unknown, the slight obesity very probably means a small or no hump. Another name would then have to be applied to the more humped and swollen form. We would then have as an alternative to the above:

(*a*) **Ptychobranchus occidentale** (Conrad). Displacement of beak 10 degrees or less.
Unio occidentalis Conrad, 1836. Displacement 0 degrees.
Ptychobranchus clintonensis Simpson, 1900.
Ptychobranchus clintonense Simpson, 1914.
(*b*) Dr. Ortmann has suggested the name of **Ptychobranchus cameloides.** Displacement of beak over 10 degrees.
Lampsilis occidentalis Simpson, 1914.

It is probable that the latter is the correct arrangement, *occidentale* being that form with a beak displacement of 10 degrees or less, or else that form with an obesity of 33 percent or less. This would include Conrad's *occidentalis* on either basis. Another difference between the two forms, though not without considerable exception, is that the more swollen form has, in general, clearer and stronger rays on the shell. Both Simpson's more swollen and flatter shells come from the Little Red River, Arkansas; and Conrad's specimen comes from the Currant River in the same state. The species appears to grow flatter in the White River and its tributaries than in the Red or the Arkansas River and their tributaries; the latter streams, however, are larger.

In so far as the material permits, we may say of this group that the more swollen forms with a more pronounced hump are to be found in the larger streams, and that the flatter forms with practically no hump are confined to the smaller rivers. Of course, it may be that the reason why the flatter forms are less humped is the method of measurement. Since the length is measured parallel to the hinge-line, a greater displacement of the beak would mean a shorter length and hence greater obesity. However, this does not affect the fundamental principle involved, which will hold whether obesity or amount of displacement of the beak be the character chosen.

The method of determining the amount of displacement was as follows. If a shell be measured parallel to the hinge-line (L), and then the total length of the shell be taken (C), the cosine of the angle α can be easily found by dividing L by C. This angle gives the amount of displacement of the beak, for as the beak is placed further forwards, L becomes less and α increases. If L and C correspond, then α is equal to 0 degrees. The following diagram will explain the method of measurement.

Measurement of all the shells of this group (42) fails to show any relation between obesity and age. This may be due to an insufficient amount of material.

5. Group of *Ptychobranchus greenii* (Conrad). (78 shells.)

(*a*) **Ptychobranchus greenii flavescens** (Lea). Obesity 38.5 percent or less.

Unio flavescens Lea, 1848. Obesity 38.4.

Here also belong one of the specimens measured by Simpson (1914) as *Ptychobranchus greeni,* obesity 34.9, and two of the specimens which he considers under *Ptychobranchus foremianium,* obesity 35.1 and 37.1.

(*b*) **Ptychobranchus greenii** (Conrad). Obesity more than 38.5 percent, but less than 41.3 percent.

Unio greenii Conrad, 1836. Obesity 41.1.
Unio velatus Conrad, 1854. Obesity 39.6.
One of the *Ptychobranchus greeni* of Simpson. Obesity 40.8.

(*c*) **Ptychobranchus greenii foremianium** (Lea). Obesity 41.3 percent or more.

Unio foremianius Lea, 1842. Obesity 41.8.
Unio simplex Lea, 1848. Obesity 45.1.
Unio woodwardianus Lea, 1859. Obesity 46.5.
Ptychobranchus foremianium Simpson, 1914. Obesity 45.7; 49.1; the other two specimens are *flavescens.*
Two of the specimens of *Ptychobranchus greeni* Simpson, 1914. Obesity 45.0 and 50.0.

The reason for forming three divisions of this group is that the specific name was originally applied to the intermediate form. In addition to the difference in obesity, it may be said that, generally speaking, the more swollen form—*i.e., foremianium*—is more triangular in shape, and possesses a lighter epidermis, more marked by blotches than is true of the flatter form. But there are many exceptions to this statement; many of the *foremianium* type, for example, being practically free from any markings. There is also probably a difference in distribution of these races. *Flavescens* is found mainly in the Cahaba, Black Warrior, and Tallapoosa Rivers, although occasionally appearing in the Coosa. Lea's specimen comes from the Black Warrior River. *Greenii* is to be found in all these streams; Conrad's *greenii* comes from the Black Warrior, his *velatus* from the St. Fois River. *Foremianium* is practically confined to the Coosa and its tributaries, though occasionally occurring in other streams. Lea says that his *simplex* comes from the Black

Warrior River; however, the measurement of obesity, 45.1, is much greater than that of any of the dozen specimens of the Black Warrior which are in the Museum collection; shells of this size occur in these specimens only in the lower Coosa. Lea's *foremianius* comes from the Coosa River, and his *woodwardianus* from the headwaters of the Coosa, and from the Etowah and Conasauga Rivers.

Examination of Tables I to IV will show clearly the greater obesity which shells of this species attain in the larger rivers. Furthermore, the younger shells tend to be more swollen than the older ones.

6. Group of *Lampsilis orbiculata* (Hildreth). (74 shells.)
    (*a*) **Lampsilis orbiculata** (Hildreth). Obesity 55 percent or less.
        Unio orbiculatus Hildreth, 1828. Obesity 70.0 (?).
        Unio crassus Conrad, 1836. Obesity 48.3 ♂.
        Lampsilis orbiculata Simpson, 1914. Obesity 40.0 ♂; 47.7 ♀.
        Lampsilis higginsi var. *grandis* Simpson, 1914. Obesity 42.8♂; 52.7 ♀.
    (*b*) **Lampsilis orbiculata higginsii** (Lea). Obesity more than 55 percent.
        Unio higginsii Lea, 1862. Obesity 59.0 ♂.
        Lampsilis higginsi Simpson, 1914. Obesity 56.0 ♂; 57.1 ♀.

Hildreth's measurement of 70 percent for the obesity of his specimen is evidently an error. None of the seventy-four shells measured for this group exceed 66 percent; and Dr. Ortmann states that he has never seen a shell of this group as swollen as that given by Hildreth. For these reasons Hildreth's figure has been disregarded in the above classification. If his measurement were correct, it would necessitate the formation of probably three varieties, with *orbiculata* as the most swollen. This is directly contrary to the accepted nomenclature of a flat *orbiculata* and a more swollen *higginsii.*

There seems to be a slight tendency for the more swollen forms to have a lighter epidermis. The localities given for *orbiculata* are Ohio, Indiana, and Illinois, usually not farther south; and for *higginsii,* Muscatine, Iowa. Hildreth's specimens come from the Muskingum River.

In *Lampsilis* the distinction between the sexes is quite easily seen in the shells of most specimens; this gives an opportunity to determine if there is any correlation between sex and obesity. Allowing for the small number of specimens, there appears to be a positive correlation in this species between highly obese and female shells. This result was obtained by considering the sexes separately, after having grouped them without such distinction. The means are as follows:

Stream-flow	All shells	Male shells	Female shells
0–3,249	51.0	50.0	51.5
3,250–8,249	.....	.....	.....
8,250–25,249	47.334	43.0	50.0
25,250–40,249	54.640	51.0	56.286
40,250 and over	50.667	48.462	54.0

In every case the female shells have a higher average obesity than do the shells of both sexes taken together.

Although the degree of obesity seems to form a continuous series, yet it can not be said that obesity is, to any great extent, dependent upon the size of the stream (Table I). Whatever correlation there is between obesity and age shows that the younger shells are less swollen (Table II), a phenomenon which is just the opposite to most of the cases heretofore considered.

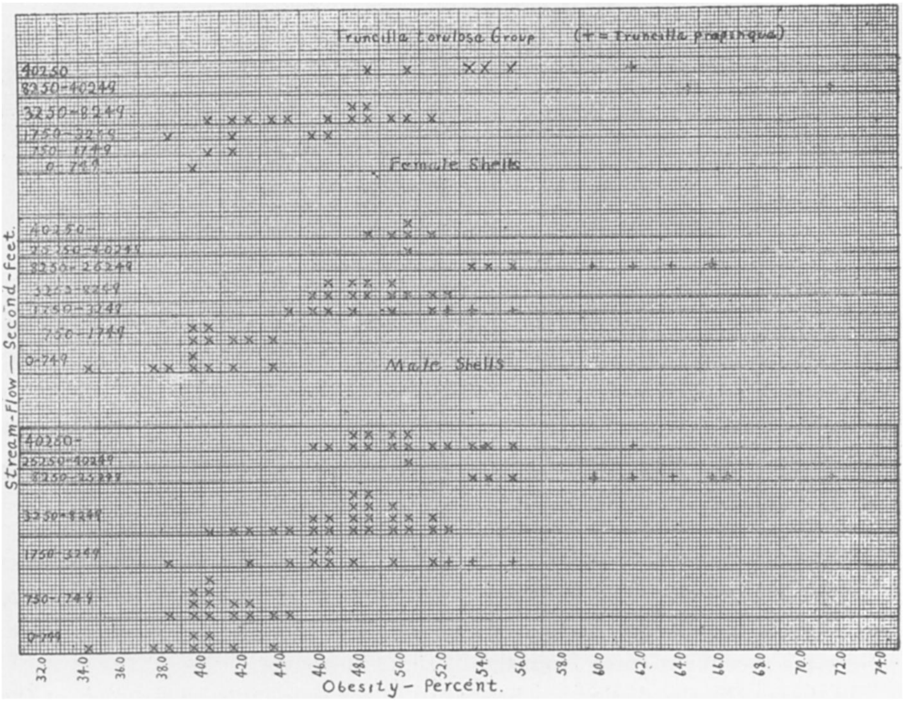


FIG. 5. Distribution of obesity in the *Truncilla torulosa* group. At the bottom is shown the distribution for the group as a whole, and above for each of the two sexes separately. The greater obesity of the male shells can be seen, as well as the lack of intergrading forms between *T. propinqua* (represented by +) and the rest of the group.

7. Group of *Truncilla torulosa* (Rafinesque). (93 shells.)

(*a*) **Truncilla torulosa gubernaculum** (Reeve). Obesity 49 percent or less; tubercles poorly developed.

Unio gubernaculum Reeve, 1868. Reeve pictures a female shell, but gives no dorsal view; hence we can not know the obesity of his specimen.

Truncilla perplexa Simpson, 1914. This includes the flatter of his three specimens. Obesity 44.8 ♂; 41.4 ♀. However, we know nothing about the development of the tubercles on these shells.

(*b*) **Truncilla torulosa** (Rafinesque). Obesity more than 49 percent; tubercles well developed.

Unio perplexus Lea, 1831. Obesity 57.0 ♂.

Unio gibbosus Conrad, 1836. Obesity 55.9 ♂.

Truncilla perplexa Simpson, 1914. Obesity 56.0 ♂. The other two specimens are *gubernaculum.*

Truncilla torulosa Vanatta, 1915. Obesity 51.5; 55.3; 62.5.

The first two of these are the *torulosa* of Rafinesque; the last is Rafinesque's *gibbosa.*

(*c*) **Truncilla propinqua** (Lea). Obesity more than 52.5 percent. Tubercles intermediate in development between those of *torulosa* and *gubernaculum.*

Unio propinquus Lea, 1862. Obesity 61.3 ♂.

Truncilla propinqua Simpson, 1914. Obesity 60.0 ♂; 62.2 ♂; 55.2 ♀; 57.8 ♀.

Truncilla propinqua does not intergrade with the other two forms, in so far as obesity is concerned. Hence it is considered as a separate species. For any given size of stream, the most swollen shells are apt to be *propinqua;* and there is a definite break between them and the less obese forms, which seem to constitute a more or less intergrading series of their own. *Propinqua* shells have not entered into the calculations or the curves and are distinctly marked in figure 5.

Lea's specimen of *propinquus* came from the vicinity of Tuscumbia, Alabama; the forms considered in the present report come from the vicinity around the lower Clinch. Conrad gives as the habitat of *torulosa* the Wabash (?), the Scioto (?), and the Tennessee as far south as Florence, Alabama. The specimens measured in this report have all come from the lower Tennessee; the *gubernaculum* shells are from the tributaries of the upper Tennessee.

The relation between degree of obesity and size of stream is clearly seen (figure 5). The flatter forms of this group are to be found in the smaller streams; the more swollen shells in the larger streams. In this group the male shells seem to be more swollen. The following is a table of means:

Stream-flow	All shells	Male shells	Female shells
0–749	39.556	39.5	40.0
750–1,749	41.0	41.25	41.0
1,750–3,249	45.8	47.667	43.0
3,250–8,249	47.44	48.667	46.308
8,250–25,249	54.667	54.667	.....
25,250–40,249	50.0 (1 shell)	50.0	.....
40,250	50.133	50.0	52.4

This is just the opposite of what was found in *Lampsilis orbiculata,* where the female shells were more swollen.

With this group the prominence of the tubercles was also measured by giving arbitrary numbers to the various shells, based on tubercle development. Those shells having no or very slight tubercles were placed in class 1; those with the strongest tubercles in class 6. Figure 6 shows that the larger streams have shells with the strongest tubercles, considering *torulosa* and *gubernaculum*. *Propinqua* specimens are more or less intermediate in

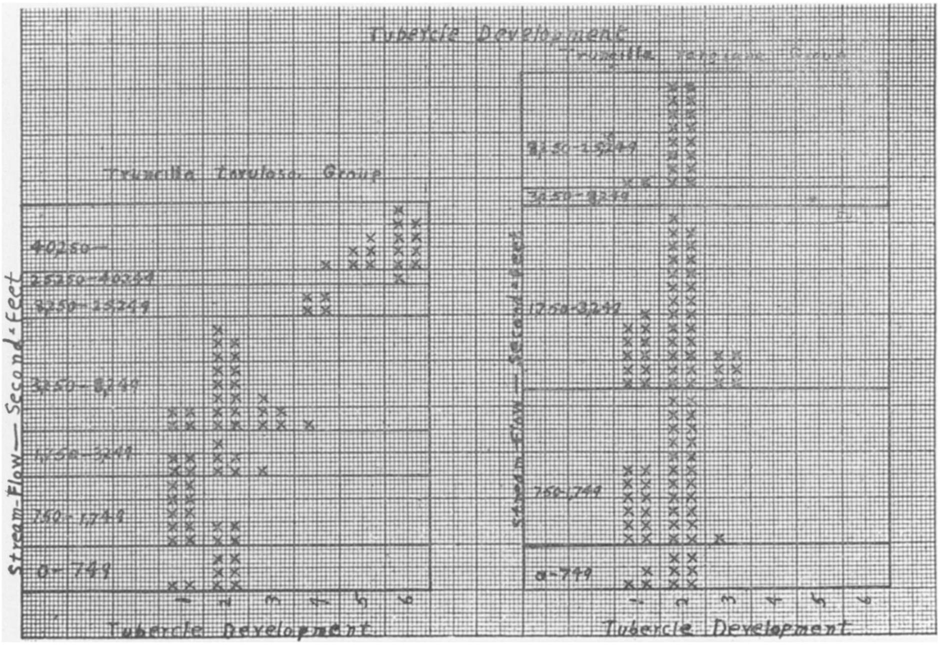


FIG. 6. Distribution of tubercle development in the two *Truncilla* groups. The numbers on the base-line represent degrees of tubercle development: a shell graded 1 has no or practically no tubercles; a shell graded 6 is strongly tuberculated. The correlation between strong tubercle development and large stream-flow on the one hand, and between lack of tubercles and small stream-flow on the other hand, is clearly seen.

strength of tubercles and position on the stream, even though they are not intermediate when grouped for obesity.

For this group there is apparently little correlation between age and obesity.

8. Group of *Truncilla rangiana* (Lea). (108 shells.)
   (*a*) **Truncilla rangiana** (Lea).
      Unio rangianus Lea, 1839. Obesity 44.4 ♀.
      Truncilla perplexa var. *rangiana* Simpson, 1914. No measurement given.
   (*b*) **Truncilla sampsonii** (Lea).
      Unio sampsonii Lea, 1862. Obesity 58.7 ♂.
      Truncilla sampsonii Simpson, 1914. Obesity 55.8 ♂; 64.5 ♀.

Lack of connecting material and of specimens of the more swollen form prevents making any statement as to the limits of these species, or as to their distinctness. There are only three clearly recognized *sampsonii* in the collection, and for these no locality is known. Besides being more swollen, *sampsonii* differs from *torulosa* in having the marsupial swelling of the female the same color as the rest of the shell. The locality given by Lea is the Wabash River, near Harmony, Indiana. *Sampsonii* is more obese than *rangiana;* the female of neither is dark green behind, thus differing from the *torulosa* group.

The figures for *rangiana* alone, show a slight increase in obesity in the larger streams. Also there is a very slight increase in prominence of tubercles in the larger streams, a difference so small that it is probably not significant. *Rangiana* is very poorly tuberculated. The male *rangiana* are more swollen than the female.

Stream-flow	All shells	Male shells	Female shells
0–749	48.667	50.0	47.5
750–1,749	47.838	47.905	47.333
1,750–3,249	46.476	47.739	48.681
3,250–8,249	.....	.....	.....
8,250–25,249	49.889	50.154	49.2

For *rangiana* there is no correlation between obesity and age.

Discussion

It should be noted in particular that because a correlation between degree of obesity and size of the stream has been found it does not follow that the stream size is the cause of the change in shape of the shell. It seems certain that other factors enter in; in fact, it may be that stream size has nothing to do with obesity except indirectly; that is, that other conditions besides size—conditions which, however, occur in large streams—are the direct cause. This seems probable when it is remembered that lake and canal forms are quite swollen, regardless of the size of the stream as measured in second-feet. In lakes and canals, big-stream conditions are duplicated except for size. In large streams the beds are usually of mud, and quite smooth; the water is apt to be softer and freer from mineral matter than in the headwaters (Ohio St. Bd. Health, 1898); the amount of silt is greater in large streams (Danglade, 1921); the kind and amount of food, as well as the temperature, are different in small and large streams (Grier, 1920*a*). Any or all of these conditions may be the ones which determine the character of the mussel fauna at any definite locality. Furthermore, the character of the pre-glacial drainage, as in *Amblema perplicata,* may influence the occurrence of intergrades.

Wilson and Clark (1914) suggest that the flatter forms are better adapted for crawling into the gravel and withstanding the strong current of small streams, and that the more swollen forms are better suited for the soft mud and weak current of large streams where greater inflation means more buoyancy. This suggestion is of doubtful value; it is hard to see how a difference in obesity of a few percent will increase the buoyancy of the shell to any appreciable extent. In fact, it is probable that rapidity of flow and the character of the bottom are not very important factors. Highly swollen shells occur in the Ohio River; yet the bottom for a good part of the distance is sand and gravel, and not mud at all. Furthermore, shells are quite apt to be found in riffles or on sand banks of the larger streams and not on the mud bottom or in deep water. Yet such shells are highly swollen.

It may be that the degree of obesity is not an adaptive character at all, but is merely connected with another character which may be adaptive or else more directly influenced by stream conditions. Isely (1913) has shown that little migration occurs among the mussels after they leave the fish; the *Lampsilis* group, however, tends to move more than the *Quadrulas.* This may explain the lack of correlation between obesity and stream-flow in many instances in the former group. It seems probable that migration, either before or after the parasitic stage, must occur, in some instances to a considerable extent, as in the case of the small streams entering the Tennessee near Florence, Alabama. Of course, other factors of distribution may have something to do with this phenomenon. The fact of greater obesity in youth for most shells indicates a differential growth-rate; shells do not tend to grow, each year, proportionately as much in diameter as in length.

Perhaps the most important question raised by this discussion is that of the heritability of these variations. If they are not inheritable, but solely the result of growth in a particular environment, how do the more swollen forms come to be found in the small streams which are tributary to large rivers; *e.g.,* near Florence, Alabama? Adult shells migrate very little. Furthermore, young shells, only a year or so old, are more obese in larger streams than shells of the same age in smaller rivers. Yet the effect of the environment on these young shells can not have been registered very noticeably in one year's growth. On the other hand, if these characters are inherited, how can one explain such peculiarities of distribution as that of *Ptychobranchus greenii flavescens,* a flat form, which occurs in the Black Warrior, the Cahaba, practically skips the Coosa, and turns up again in the Tallapoosa; though these rivers are all more or less parallel, empty into a common stream—the Alabama, and lie with the Coosa between the Cahaba and the Tallapoosa? Furthermore, why do the same size streams, though belonging to entirely different drainage systems, *usually* have shells of a comparable degree of obesity?

This is a question to be settled by experiment. Outside of Lang's work on *Helix* (Adams, 1915), practically nothing has been done experimentally on this phase of the problem of inheritance in molluscs. This is a field practically untouched, which promises excellent results for any one who enters upon it.

CONCLUSIONS

For the species considered:

1. Shells of the same species often change in shape according to the size of the stream in which they occur. Shells of smaller streams are less swollen than those of larger streams.
2. Certain groups of shells show this correlation much more strongly than do others; in some cases there is apparently no relation between the size of the stream and the degree of obesity.
3. Other factors in addition to the size of the stream apparently enter into the determination of the degree of obesity.
4. For most species considered, young shells are more swollen than older ones.
5. There is frequently a correlation between sex and obesity; either the male or the female shell may be the more swollen.
6. In some cases the development of the tubercles is greatest in the large-stream forms; in other cases tubercle development is the same throughout the stream.
7. Usually the flattest and the most swollen forms are connected by a complete series of intergrades.

SUMMARY

In the opinion of many investigators, certain variations of fresh-water mussels are apparently not fortuitous, but depend upon various ecological conditions. A statistical investigation proves this to be the case in some groups. A comparison of stream-flow measurements with the obesity of shells belonging to a single species shows frequently that shells in large-size streams are more swollen than those of small-size streams. Since obesity is frequently used as a specific character, and since many so-called species can

be connected by intergrades, this investigation has made clear that certain mussels, now considered separate species, are merely the different forms of a single species-group. However, it is probable that the size of the stream is only the indirect cause of any differences in obesity. Shells tend to become less obese as they grow older. Frequently one sex has a more swollen shell than the other. It is uncertain whether or not these variations, except those connected with sex, are inherited.

Literature Cited

Adams, C. C.

'15 The Variations and Ecological Distribution of the Snails of the Genus *Io*. Mem. Nat. Ac. Sci., XII, Pt. 2.

Baker, F. C.

'98 The Mollusca of the Chicago Area—The Pelcypoda. Chi. Ac. Sci. Bul., III, Pt. 1.

Coker, R. E.

'14 Water-Power Development in Relation to Fishes and Mussels of the Mississippi. Bur. Fish. Doc. 805, App. VIII to Rep. U. S. Com. Fish. for '13.

Conrad, T. A.

1835–40 Monography of the Family Unionidae or Naiades of Lamarck (Fresh water Bivalve Shells) of North America.

1850 Descriptions of New Fresh-Water and Marine Shells. Jour. Ac. Nat. Sci. Phila., Vol. 1, 2d Ser., p. 4ff., pp. 275–280. Jan., 1850.

1854 Descriptions of New Species of Unio. Jour. Ac. Nat. Sci. Phila., Vol. 2, 2d Ser., p. 4ff., pp. 295–300. Feb., 1854.

Danglade, E.

'14 The Mussel Resources of the Illinois River. Bur. Fish. Doc. 804, App. VI to Rep. U. S. Com. Fish. for 1913.

Grier, N. M.

'20*a* Morphological Features of Certain Mussel-Shells Found in Lake Erie, Compared with those of the Corresponding Species Found in the Drainage of the Upper Ohio. Ann. Car. Mus., Vol. 13, Nos. 1–2, pp. 145–182.

'20*b* Sexual Dimorphism and Some of its Correlations in the Shells of Certain Species of Najades. Amer. Mid. Nat., Vol. 6, pp. 165–171.

'20*c* Variations in Nacreous Color of Certain Species of Naiades Inhabiting the Upper Ohio Drainage and their Corresponding Ones in Lake Erie. Am. Mid. Nat., pp. 211–243, July–Sept.

'20*d* Variation in Epidermal Color of Certain Species of Najades Inhabiting the Upper Ohio Drainage and their Corresponding Ones in Lake Erie. Am. Mid. Nat., pp. 247–285. Nov.

Hildreth, S. P.

1828 Observations on, and Descriptions of the Shells Found in the Waters of the Muskingum River, Little Muskingum, and Duck Creek in the Vicinity of Marietta, Ohio. Am. Jour. Sci. and Arts, Vol. 14, No. 2, pp. 276–291. July.

Isely, F. B.

'11 Preliminary Note on the Ecology of the Early Juvenile Life of the Unionidae. Biol. Bull., Vol. 20, No. 2, pp. 77–80.

'13 Experimental Study of the Growth and Migration of Fresh-Water Mussels. Bur. Fish. Doc. 792, App. III to the Rep. U. S. Com. Fish.

Israel, W.

'10 Die Najadeen des Weidagebietes. Beitrage zur Kenntniss der Mitteleuropaischen Najadeen, No. 4, pp. 49–56. July, 1910.

Lea, Isaac

1831–48 Observations on the Genus *Unio*. Tr. Am. Phil. Soc. Obs. I–IV.

1858–74 Observations on the Genus *Unio*, etc. Jour. Ac. Nat. Sci. Phila. Obs. VI–XIII.

Meek, S. E. and Clark, H. W.

'12 The Mussels of the Big Buffalo Fork of the White River, Arkansas. Bur. Fish. Doc. 759.

Ohio, Health Board of

1897–98 Preliminary Report of an Investigation of Rivers and Deep Ground-Waters of Ohio as Sources of Public Water Supplies.

Ortmann, A. E.

'09 A Preliminary List of the Najades of Western Pennsylvania. Ann. Car. Mus., Vol. 5, pp. 192ff.

'12*a* Notes Upon the Families and Genera of the Naiades. Ann. Car. Mus., Vol. 8, No. 2.

'12*b* The Geological Origin of the Fresh-Water Fauna of Pennsylvania. Top. and Geol. Survey of Pa., pp. 130–149.

'18 The Naiades (Fresh-Water Mussels) of the Upper Tennessee Drainage With Notes on Synonomy and Distribution. Proc. Am. Phil. Soc., Vol. 57, No. 6, pp. 522–626.

'20 Correlation of Shape and Station in Fresh-water Mussels (Naiades). Proc. Am. Phil. Soc., Vol. 59, No. 4, pp. 270–312.

Pennsylvania, Water Supply Commission of

1905–17 Reports.

Reeve, L. A.

1868 Conchologia Iconica or Illustrations of the Shells of Molluscous Animals. Vol. 16.

Simpson, C. T.

1900*a* On the Evidence of the Unionidae Regarding the Former Courses of the Tennessee and Other Southern Rivers. Science, N. S., Vol. 12, pp. 133–136.

'00*b* New and Unfigured Unionidae. Proc. Ac. Nat. Sci. Phila., pp. 74–86.

'14 A Descriptive Catalogue of the Naiades, or Pearly Fresh-Water Mussels.

United States Geological Survey

1899–1917 Water Supply Papers, Nos. 36–458.

Utterback, W. I.

'16 Naiades of Missouri. Am. Mid. Nat., 4.

Vanatta, E. G.

'15 Rafinesque's Types of Unio. Proc. Ac. Nat. Sci. Phila., pp. 549–559.

Wetherby, A. G.

1882 On the Geographical Distribution of Certain Fresh-Water Mollusks of North America and the Probable Causes of their Variation. Am. Jour. Sci., Vol. 23, 3d Ser., pp. 76–77; 203–212.

Wilson, C. B. and Clark, H. W.

14 The Mussels of the Cumberland River and its Tributaries. Bur. Fish. Doc. 781.